# CORRELATION BETWEEN CERTAIN SPECIES OF PUCCINIA AND UROMYCES[1]

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(With Plates 70 and 71, Containing 12 Figures)

There are many interesting taxonomic problems which have arisen in the work of preparing the Uredinales for North American Flora. One of these problems, which has been supplemented somewhat by cultures and field observations, bears directly upon the relationship existing between *Puccinia* and *Uromyces*. To bring out one feature of this relationship more clearly than heretofore presented the writer has prepared this paper, pointing out certain species in the two genera which are conspicuous because of their apparent morphological similarity and of their occurrence upon the same or closely related hosts in both gametophytic and sporophytic stages. The similar geographical distribution of these correlated species appears in most cases to afford some additional support to this relationship.

A brief statement of the treatment of *Uromyces* and *Puccinia* by the leading workers on the rusts, from Persoon's time to the present, is here included for the purpose of a better understanding of the taxonomic development of these genera.

Persoon in 1794[2] was the first to publish any clearly defined work on fungi in which the Uredinales were included. In this work he brought forward the name *Puccinia,* a name first used by Micheli, a prebinomial author, and applied it to species of *Phragmidium* and those of other genera including three species of *Puccinia* as we now use that genus. In the same work the genus *Uredo* was established which contained four species now referable to as many genera. The second species was *Uredo Fabae* which is undoubtedly a *Uromyces*. In a later work[3] by the same

[1] Read before the American Phytopathological Society at the Washington meeting, Dec. 28, 1911.

[2] Neues Mag. Bot. 1: 93. 1794.

[3] Syn. Fung. 1: 220–230. 1801.

author there were three species now referable to the genus *Puccinia* included under that genus along with species representing at least three other genera, and under *Nigredo,* a name which he established as a subgenus of *Uredo,* there were several species which would now be referred to *Uromyces.*

The principal workers who followed Persoon were Schumacher in 1803, Willdenow in 1804, and DeCandolle in 1805. The last author made a slight variation from Persoon's classification in his admirable systematic work on the French flora.[4] He divided the genus *Puccinia* into three sections, the first of which included several species of *Phragmidium.* The second section contained 13 species, the majority of which are referable to *Puccinia* as now used. Under the third section, which he characterized as being similar to *Puccinia* but having one-celled spores, six species were listed all of which are now referred to *Uromyces.*

After DeCandolle came Link, who in 1809[5] established the genus *Caeoma* corresponding to *Uredo* of Persoon. It was divided into five sub-genera. Under the sub-genus *Caeomurus* he placed DeCandolle's third section of *Puccinia* with one-celled spores, now properly referred to *Uromyces.* In 1816[6] Link separated the genus *Phragmidium* from *Puccinia* under which it had been previously included and left under *Puccinia* several species now properly referred to this genus. In this same work *Caeoma* was changed to *Hypodermium* and *Caeomurus* to *Uromyces* but their generic relation to each other remained as in 1809. In 1825[7] he published his third important contribution, in which the rusts were classified under several genera which included *Caeoma, Puccinia, Triphragmium, Phragmidium, Podisoma,* and *Gymnosporangium.* There were 48 species listed under *Puccinia,* practically all of which are now referable to that genus. *Caeoma* was divided into four sub-genera, namely: *Uredo, Aecidium, Ceratitium* and *Peridermium.* The first contained 113 species many of which were probably in the uredinial stage. There appears to be no disposition of species belonging to *Uromyces* except under this sub-genus.

[4] Flora Francaise **2**: 218–236. 1805.
[5] Ges. Nat. Freunde Berlin Mag. **3**: 6. 1809.
[6] Ges. Nat. Freunde Berlin Mag. **7**: 28–30. 1816.
[7] Willd. Sp. Plant. **6**[2]. 1825.

Link's 1816 classification was followed by Nees in 1817 and by S. F. Gray in 1821. Later came a series of authors, Schweinitz, Wahlenberg, Castagne, Léveillé and the Tulasnes, who in their disposition of *Uromyces* followed the methods of no one author but who endeavored to follow the combined good points of Persoon, DeCandolle and Link, which resulted in general confusion.

It remained for Fries,[8] the "Father of Mycology," to take up in 1846 the name *Uromyces,* which had been technically established as a genus by Unger[9] in 1833, and to place it in its present generic use. He made the noteworthy statement "Plurimae Pucciniae analogae respondent," a fact which none of the later urediniologists have refuted, and one which touches closely upon the subject of this paper. Schroeter[10] clearly brings out this analogous relation when he divides the genus *Uromyces* into biologic forms as eu-, brachy-, -opsis, micro-, and lepto-, in exactly the same manner as he did with the genus *Puccinia.*

Magnus[11] has called attention to the close morphological relationship existing between *Puccinia* and *Uromyces* on species of *Rumex* and has shown that in these species the urediniospores of the two genera intergrade in size and germ-pore characters on different species of host plant so that it is difficult to separate them in the uredinial generation.

Fischer in 1904[12] pointed out that a closer relationship existed between certain species of the genera *Puccinia* and *Uromyces* than existed in either genus alone, a fact which Arthur also observed and commented on in his "Classsification of the Uredinales."[13] Later in an article on "Reasons for Desiring a better Classification of the Uredinales"[14] Arthur calls them "parallel genera" differing only in the technical character of their teliospores.

McAlpine in his fine work on "The Rusts of Australia"[15] in speaking of *Puccinia* says: "The presence of mesospores in a

[8] Summa Veg. Scand. 1: 514. 1846.

[9] Exanth. Pfl. 277. 1833.

[10] Abh. Schles. Ges. 48: 8–11. 1869. Schroeter in Cohn, Krypt. Flora Schles. $3^1$: 229–313. 1887.

[11] Abh. Bot. Brand. 38: 11–14. 1896.

[12] Beitr. Krypt. Schweiz. $2^2$: xlvi. 1904.

[13] Result. Sci. Congr. Bot. Vienne 334. 1906.

[14] Jour. Myc. 12: 150–151. 1906.

[15] The Rusts of Australia 26. 1906.

species would seem to indicate its still close relationship to *Uromyces,* and that its separation from the parent form has not yet proceeded sufficiently far to obliterate every trace of its former connexion."

Hariot in his "Les Uredinees"[16] says that the autonomy of *Uromyces* is a difficult question and that if it is to be kept as a distinct genus it is only in order to follow the custom and to facilitate determinations. This statement seems very much to the point, but the author does, however, treat the two genera as distinct in this work.

P. & H. Sydow in their monograph of *Uromyces*[17] state that the genus differs from *Puccinia* only in the number of cells in the teliospore, and they cite several comparative examples of both the gametophytic and sporophytic generations of the two genera to show this similarity.

It is seen, then, that the name *Puccinia* was first applied to a *Gymnosporangium* by Micheli, was later applied by Persoon to *Phragmidium* with which a few species of *Puccinia* were included, and was in 1816 separated by Link from *Phragmidium* and made a genus as we now use it.

The species of rusts now referable to the genus *Uromyces* were first included by Persoon and his followers under *Uredo.* Later it was included as a sub-genus of *Puccinia* by DeCandolle, and was finally established technically as a genus by Unger in 1833 and put into general use by Fries in 1846. Since Fries' work all uredinologists have treated it as a distinct genus differing from *Puccinia* especially in its teliosporic character.

The present paper is what the writer believes to be the first attempt to list the correlated species in *Puccinia* and *Uromyces* and is limited to a discussion of a few of the more prominent types of correlation in the long-cycle forms only.

The writer acknowledges the generous aid and counsel of Dr. J. C. Arthur, without which the work would be impossible, and grateful thanks are due Dr. F. D. Kern for many helpful suggestions.

The first example to attract special attention was furnished by

[16] Les Urédinées 20. 1908.

[17] Monog. Ured. 2: vi–xi. 1909.

Mr. W. P. Fraser[18] of Pictou, Nova Scotia, when he made sowings in the spring of 1910 of teliospores of *Uromyces Peckianus* Farlow on *Atriplex patula* and *Chenopodium album,* both of which produced infection and formed aecia of the same type as those of *Puccinia subnitens* Diet. on the same hosts. This extremely interesting result led to a careful comparison of the two rusts with results as follows: *Puccinia subnitens* Diet., is a rust on *Distichlis spictata* (L.) Greene and has its aecia on a large number of Chenopodiaceous, Capparidaceous and Cruciferous hosts,[19] which include *Atriplex, Beta, Cleome, Capsella, Chenopodium, Lepidium, Sarcobatus,* etc. The aecia are grouped and have erect peridia with peridial cells rhomboidal and in radial sections much thickened in the outer wall. On comparing the aecia of *Uromyces Peckianus* it was found that they were identical in all discernible morphological characters. The chief interest, however, lies in a comparison of the urediniospores, the morphology of which has been of greatest use in the study of the grass and sedge rusts. The urediniospores of *Puccinia subnitens* measure 18–24 by 19–26 $\mu$, are pale cinnamon-brown with a wall about 2 $\mu$ thick, very finely verrucose, the pores 6, scattered. The urediniospores of *Uromyces Peckianus* measure 16–21 by 18–24 $\mu$, are pale cinnamon-brown with a wall about 2.5 $\mu$ thick, very finely verrucose, and have 6 scattered pores. The teliospores of the two rusts possess no differential characters except, of course, number of cells and consequent size.

The distribution of the two is interesting. The telial host of both, *Distichlis spicata* (L.) Greene, grows in salt marshes on the Atlantic and Pacific coasts and in saline soil in the interior. *Uromyces Peckianus* is known only from the coastal regions while *Puccinia subnitens* on the other hand is an interior form having been collected at only one point on the coast and that at Lewes, Delaware. The reason for this is speculative at present, but it seems probable that the one-celled form is less adaptive to varying conditions of soil and temperature than the two-celled form and so has thus far been unable to thrive in the interior.

[18] Mycologia 3: 72–74. 1911.

[19] Bot. Gaz. 35: 19. 1903; Jour. Myc. 11: 55. 1905; 12: 16. 1906; 13: 197. 1907; 14: 15. 1908; Mycologia 1: 234. 1909; 2: 225, 1910: 4: 18. 1912; 4: 54. 1912.

The next species to attract particular attention and which are undoubtedly correlated are a *Puccinia* passing under several names (*P. Caricis-Asteris, P. Caricis-Solidaginis, P. Caricis-erigerontis*) on various species of *Carex,* having aecia on *Aster, Solidago, Erigeron,* and close relatives,[20] and *Uromyces perigynius* Hals. (*U. caricina* E. & E.) on several species of *Carex* which is known to have its aecia on *Solidago* and *Aster.*[21] The aecia of the two species appear identical and a careful microscopical study reveals that the peridial cells and aeciospores cannot be differentiated. The urediniospores of the *Puccinia* measure 14–19 by 18–24 $\mu$, are light cinnamon-brown with a wall about 1.5 $\mu$ thick, moderately echinulate and have 2 superequatorial pores. A comparison of the urediniospores of *Uromyces perigynius* shows that they are identical in all their characters with the *Puccinia* form. The teliospores of the two species also possess identical characters except number of cells, having thin walls and rather thick apices. The distribution of the two is practically the same, extending across the northern half of the United States and into Canada. Three of the telial hosts, *Carex intumescens* Rudge, *C. scoparia* Schk., and *C. tribuloides* Wahl. are the same for both species.

A rust on species of *Andropogon, Puccinia Ellisiana* Thüm., has been in cultures[22] four different years on various hosts without success. It is a form widely distributed throughout the United States east of the Rocky mountains and in Mexico, and had puzzled us much until Dr. J. F. Brenckle, of Kulm, North Dakota, wrote on June 5, 1911, that he had found aecia on *Viola* near *Puccinia Ellisiana.* In a later communication he mentioned evidence to verify this probable connection. The suggestion seems very likely for in the Arthur Herbarium there are collections of aecia on *Viola* within the range of this rust which are out of the range of the *Uromyces* on *Andropogon* and which have peridial cells and aeciospores that are clearly differentiated, when carefully compared microscopically, from the autoecious rusts on *Viola.* On a careful study of *Puccinia Ellisiana* we find that

[20] Jour. Myc. 8: 53–54. 1902; Bot. Gaz. 35: 15, 21. 1903; Jour. Myc. 11: 58. 1905; 12: 15. 1906; 14: 13. 1908; Mycologia 1: 233. 1909; 2: 224. 1910.

[21] Mycologia 4: 21. 1912.

[22] Jour. Myc. 14: 10. 1908; Mycologia 1: 231. 1909; 2: 220. 1910; 4: 9. 1912.

it is apparently correlated with *Uromyces pedatatus* (Schw.) Sheldon. It has urediniospores which measure 18–20 by 19–23 μ, with walls about 3 μ thick, usually slightly thicker above, very finely and closely verrucose-echinulate, and have 4 or sometimes 3 equatorial pores. The urediniospores of *Uromyces pedatatus* possess no differential characters from those of *Puccinia Ellisiana* and have the same number and arrangement of pores. The teliospores of the two have the same general shape and wall thickness and so we venture to predict that Dr. Brenckle's observations are entirely correct and that *P. Ellisiana* has *Viola* for its aecial host.[23] The telial hosts of *Uromyces pedatatus* are restricted so far to *Andropogon glomeratus* (Walt.) BSP. and *A. virginicus* L. with a range extending from the Atlantic coast to Arkansas and southward, while the telial hosts of *Puccinia Ellisiana* include in addition to those of *U. pedatatus, Andropogon furcatus* Muhl. and *A. scoparius* Michx. with practically the same southern range but extending further north into North Dakota and west to Colorado. Here we see the greater adaptability of the two-celled form in a wider range of hosts and distribution.

In 1901, Dr. Arthur[24] connected a rust on *Carex pubescens* with an aecium on *Ribes Cynosbati* L. which possessed in culture a white or very pale peridium in contrast to the usual orange-colored aecial forms on various species of currants and gooseberries. He named the rust *Puccinia albiperidia.* In 1910 it was found that the original telial host as well as several other telial hosts represented in the herbarium, part having been reported in cultures,[25] possessed urediniospores with the marked morphological character of one basal pore, and it was decided that *P. albiperidia* was a good morphological species having its aecia on *Ribes* spp. Very recently, however, it has been found that in the type material and in every case where the species has been cultured on *Ribes* urediniospores in more or less abundance could be found which were morphologically identical with the urediniospores of the common gooseberry-currant rust of Europe and America.

[23] Since the writing of this paper it has been communicated to the writer through Dr. F. D. Kern that Mr. W. H. Long reports having cultured a *Puccinia* from *Andropogon* upon *Viola.* Doubtless this was *Puccinia Ellisiana.*

[24] Jour. Myc. 8: 53. 1902.

[25] Jour. Myc. 10: 11. 1904; Mycologia 4: 13. 1912.

This discovery has led to the conclusion that the common form has been responsible for the successful cultures upon *Ribes* of this particular rust bearing the name *P. albiperidia* and that the rust having urediniospores with one basal pore is an unconnected form without a name. In order to discuss more readily this particular species I hereby propose the following name for it:

**Puccinia uniporula** sp. nov.

Urediniospores broadly ellipsoid, 16–23 by 25–29 μ, wall 1.5–2 μ thick, with only one pore placed near the hilum. Telia hypophyllous, scattered, roundish or oblong, 0.2–0.7 mm. long, early naked, pulvinate, dark cinnamon-brown. Teliospores broadly clavate, 15–20 by 34–48 μ, apex thickened up to 10 μ. Pedicel about once the length of spore or less.

The type is on *Carex pubescens* Muhl., collected at London, Canada, August 20, 1910, by J. Dearness. It has also been detected on six other species of *Carex,* and occurs sparingly from Newfoundland to Iowa.

In 1910, Dr. F. D. Kern[26] published the species *Uromyces uniporulus* on *Carex tenuis,* which has broadly ellipsoid urediniospores measuring 18–21 by 21–26 μ, with cinnamon-brown walls about 1.5 μ thick, rather sparsely and distinctly echinulate, and having one basal pore. The telial hosts of this rust are *Carex gracillima* Schw. and *C. tenuis* Rudge, both of which are hosts of *Puccinia uniporula.* The distribution of this species is now known locally from the New England states to Wisconsin. The aecial host of *Uromyces uniporulus* is unknown but it is undoubtedly the same as that of *Puccinia uniporula.*

The rusts on *Spartina* have been studied considerably in the past and three forms of *Uromyces* which variously intergrade have been separated, having aecia on members of the *Caryophyllaceae, Primulaceae,* and *Polemoniaceae* respectively.[27] The form of *Uromyces acuminatus* Arth., having aecia on *Steironema ciliatum* (L.) Raf. and telia on *Spartina gracilis* Trin. and *S. Michauxiana* Hitch. possesses urediniospores which are globoid, meas-

[26] Rhodora **12**: 125. 1910.

[27] Jour. Myc. **12**: 24. 1906; **13**: 193. 1907; **14**: 17. 1908; Mycologia **2**: 221. 1910; **4**: 29. 1912.

uring 23–26 by 26–30 μ, wall golden-yellow, 2–3 μ thick, very finely and sparsely echinulate, the pores being 8 scattered. *Puccinia Distichlidis* E. & E. was erroneously described as on *Distichlis maritima* Raf., the host being *Spartina gracilis* Trin. This rust has urediniospores whach are globoid, measuring 23–26 by 26–30 μ are golden-yellow with a wall 3–3.5 μ thick, very finely and sparsely echinulate, the pores being 8 scattered. The teliospores of the two rusts possess the close resemblanc of correlated forms. The distribution of the two-celled form extends from Iowa northwest to Wyoming and Montana, and of the one-celled form from Illinois west to Colorado and north to Alberta. The telial hosts of the two forms are the same. *Puccinia Distichlidis* has been cultured[28] on 21 different aecial hosts without success but not on the aecial host of *Uromyces acuminatus.* It seems, therefore, extremely probable that its aecial host is on some member of the primrose family, perhaps *Steironema,* or some member of the phlox family, but more likely the former.

Another evident case of correlation exists between *Puccinia Pammellii* (Trel.) Arth. and *Uromyces graminicola* Burr. In 1904, Dr. Arthur reported the cultures[29] of *Puccinia Panici* Diet. as the rust on *Panicum virgatum* was then called, upon *Euphorbia corollata* L. This rust has globoid urediniospores, measuring 19–23 by 21–24 μ, with a light cinnamon-brown wall about 2 μ thick, finely verrucose-echinulate, the pores are 3 or 4, usually approximately equatorial, but often scattered. The teliospores are small, somewhat thickened and rounded above.

*Uromyces graminicola* Burr. also on *Panicum virgatum* L. has been cultured[30] on 19 various hosts without success but never on *Euphorbia* to the writer's knowledge. It has globoid urediniospores measuring 15–19 by 18–23 μ which have all their other characters identical with those of *Puccinia Pammellii.* The teliospores of these forms have the same morphological resemblance which is expected in correlated species. *Puccinia Pammellii* has a distribution from Pennsylvania west to Nebraska and south to the Gulf of Mexico and *Uromyces graminicola* has practically the

[28] Mycologia 2: 219, 1910; 4: 11, 1912.

[29] Jour. Myc. 11: 56. 1905.

[30] Jour. Myc. 12: 13. 1906; Mycologia 1: 232. 1909; 4: 12. 1912.

same distribution. It seems very probable, therefore, that this one-celled form has aecia of the same character as those connected with *Puccinia Pammellii* and on an upright form of *Euphorbia*.

Several other examples have been observed which have for their telial hosts identical or closely related species of the same genus, only a mention of which is made here. Among the heteroecious forms the following have been noted:

1. *Puccinia Eleocharidis* Arth. with *Uromyces Eleocharidis* Arth., both on *Eleocharis* spp., the *Puccinia* having aecia on *Eupatorium perfoliatum*.

2. *Puccinia angustatoides* Stone with *Uromyces Rhynchosporae* Ell., both on *Rhynchospora* spp.

The following autoecious species present the same striking correlation in all their spore forms as do the heteroecious species:

1. *Puccinia heterantha* Ell. & Ev. with *Uromyces plumbarius* Peck, both on several representatives of the Onagraceae.

2. *Puccinia Gentianae* (Str.) Link with *Uromyces speciosus* Holw. on *Gentiana* spp.

3. *Puccinia Ruelliae-Bourgaei* Diet. & Holw. with *Uromyces Ruelliae* Holw. on *Ruellia* spp.

4. *Puccinia opaca* Diet. & Holw. with *Uromyces cucullatus* Sydow both on *Zexmenia* spp.

There are a few slight comparative differences worthy to be noted in a careful study of these correlated species. From a comparison of accurate measurements of a large number of urediniospores it is found that those of the *Puccinia* species are usually slightly larger and have thicker walls than those of the correlated *Uromyces* form. There is also sometimes noticed a marked difference in the vigor of the two forms, the *Puccinia* being the more vigorous in its attack upon the host plant. These differences, however, only mean that the genus *Puccinia* has a greater adaptability to environmental conditions and seems better fitted to survive than the less vigorous form. This is also brought out in the preponderance in numbers of species in the genus *Puccinia* as compared to the number in the genus *Uromyces*.

There are many correlated species among the long-cycle forms of *Puccinia* and *Uromyces* which are not mentioned in this paper.

Many southern and western species are but imperfectly understood and lack of time has prevented a careful study of some of the forms already fairly well known. It should not be inferred that every species of *Puccinia* has a correlated form in *Uromyces*. Correlation does occur frequently however, and appears not to be confined to any particular family or order of hosts, although it seems to be most common on the grasses and sedges. The reasons for these limitations appear to lie in a solution of the conditions surrounding the evolution of the rusts and their hosts, and any knowledge concerning the evolution of host and parasite undoubtedly has a close bearing upon the solution of this phase of the problem.

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## EXPLANATION OF PLATES LXX AND LXXI

The drawings were outlined with the camera lucida at a uniform scale, the reproductions representing approximately 470 diameters. In all cases the urediniospores are represented with the hilum, or attachment of pedicel, below. The urediniospores are drawn to show thickness of wall, surface markings and position and number of germ pores. The teliospores are drawn to show thickness of wall and apex, and the average length of pedicel.

Fig. 1. *Puccinia subnitens* on *Distichlis spicata.*
Fig. 2. *Uromyces Peckianus* on *Distichlis spicata.*
Fig. 3. *Puccinia Caricis-Asteris* on *Carex tribuloides.*
Fig. 4. *Uromyces perigynius* on *Carex intumescens.*
Fig. 5. *Puccinia Ellisiana* on *Andropogon furcatus.*
Fig. 6. *Uromyces pedatatus* on *Andropogon virginicus.*
Fig. 7. *Puccinia uniporula* on *Carex pubescens.*
Fig. 8. *Uromyces uniporulus* on *Carex gracillima.*
Fig. 9. *Puccinia Distichlidis* on *Spartina gracilis.*
Fig. 10. *Uromyces acuminatus* on *Spartina gracilis.*
Fig. 11. *Puccinia Pammellii* on *Panicum virgatum.*
Fig. 12. *Uromyces graminicola* on *Panicum virgatum.*